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Fine Structure of Photophores in *Gonostoma elongatum:* Detail of a Dual Gland Complex

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Abstract. *Gonostoma elongatum* Gunther 1878 is a mesopelagic fish that has numerous light-bearing organs (the photophores). Some of the photophores are unusual in that they incorporate two different glands: glands D and V. These dual gland photophores are found: (1) in the upper serial row on the body, (2) among the suborbital photophores, and (3) in the caudal photophores. In a ventral serial row of photophores, each organ possesses one gland only: gland D. Glands D and V in the upper serial photophores have secretory ducts that fuse to form a common duct that empties to the surface. Gland D, which produces a bluish light, has dioptric material that could provide both spectral reflection and filter transmission. Gland V also has dioptric material associated with it. The entire glandular complex is covered by a shield of alternately layered collagen, which has a lens-like bulge over gland D. Immediately beneath the shield are slanted, overlapping rows of dioptric material. The detailed morphology of the dual gland photophore in the upper serial row is presented and briefly compared to some of the other photophores on the fish. Noteworthy are the various arrangements of materials that can efficiently guide the light from gland D and, possibly, from gland V. The result would be a diffuse glow suitable for counter illumination.

Introduction

Throughout the oceans there is a large population of mesopelagic fishes, the so-called midwater fishes. The term "midwater" is somewhat misleading in that, even in the deepest of oceans, the average habitat depth is within the range of 300 to 1500 meters, and at night some of the fish migrate to the surface. The primary concentration is usually associated with a thermocline marking the junction of warm, actively mixed surface water and the colder, less active deeper waters. The specific gravity difference at that interface permits trapping of material that provides an ecological niche.

One very interesting adaptation of mesopelagic fishes to the darkness of their habitat is the presence of photophores (bioluminescent organs). The photophores are usually distributed in a characteristic order over the body, so much so that the pattern can be used for taxonomic identification (Grey, 1964). The anatomical morphology of the photophores ranges from the huge, complex organs in *Argyropelecus* to the simple skin photophores of *Chauliodus* (Bassott, 1966; Herring and Morin, 1978).

Gonostoma elongatum is a relatively large mesopelagic fish that possesses many of the various types of photophores, such as lateral serial, orbital, opercular, branchiostegal, and caudal (sternchase). Representative photophores from the upper lateral serial row were chosen for study.

Attention was drawn to the upper serial photophores because each has two parts, a dorsal spherical unit and a closely associated ventral unit, plate-like, silvery, and reflective. The upper unit is accepted as a glandular photophore in the usual sense and used for taxonomic purposes (Grey, 1964; Badcock, 1984), but there is no general agreement as to the nature of the lower unit. One of the first to describe it was Brauer (1908) who called it a "sack formigen Organ." In the more recent literature, it is referred to as "glandular" (Grey, 1964, and Badcock, 1984). I find no cytological descriptions of the lower gland or estimates as to its function.

Buck (1978) and Young (1983) provide extensive discussion of bioluminescence as linked to counterillumination, species and sex recognition, searchlights, lures, flashes or clouds to distract predators, and so forth. Clarke (1963) observed that most photophores in fish provide a

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light nearly matching the blue spectral value (478 nm) of residual down-dwelling light from the ocean surface. Thus, the light from the photophores could "camouflage" the fish from the sight of predators, and especially from below. This possibility is described in some detail by McAllister (1967), Herring (1982), and Denton *et al.* (1985). Details as to the spectral values of photophore light, as compared to those of the environment at oceanic depths, are provided by Denton and Herring (1978) and Herring (1984). Evidence that fish can adjust the strength of their photophore emissions to match the intensity of down-dwelling light is provided by Case *et al.* (1977), Lawry (1974), and Young and Roper (1977). As an additional comment about spectral values and their ecological import, it should be noted that the eyes of deep sea fishes have a chrysopin pigment that absorbs maximally at about 480 nm, virtually the same as the down-dwelling light and that of the photophores (see discussion by Nicol, 1989).

Gonostoma might be an exceptional fish, in that Swift *et al.* (1977) have reported a photophore spectral value of 503 nm for it, but this observation of *Gonostoma* was based on a single photophore on a single specimen that was so badly damaged the species could not be identified with certainty. More significantly, Swift *et al.* used an early spectrometric system requiring slow point by point measurement, which could lead to uncertainty. The observation need not be discarded, but it should always be qualified. Widder *et al.* (1983) used the more sophisticated optical multichannel analyzer (OMA) and surveyed spectral values emitted by some 70 marine species; the values mostly ranged from 470 to 480 nm.

This article describes in detail the histological and cytological morphology of the two units in the upper serial row of photophores in *G. elongatum* and the connection between the two. Also of note is the associated array of dioptric tissues that may guide light emission. Brief comparisons are made between the upper serial photophore and three others in the same fish: lower serial, suborbital, and caudal photophores.

Materials and Methods

The largest collections of *Gonostoma elongatum* were made on two cruises: the Woods Hole Oceanographic Institute (WHOI) RV Knorr cruise #118-4 on a transect from San Juan, Puerto Rico, to Woods Hole, Massachusetts; and the WHOI RV Oceanus cruise #183. On both trips, a 10-ft.^{2} MocNess midwater trawl was used, and the best collections were made near the outer edge of the continental shelf in the general area of the Hudson Canyon or slightly south thereof. On other trips, few random *G. elongatum* individuals were otherwise collected by using less efficient meter nets. Estimated collection depth ranged from 350 to 900 meters. The specimens were between 150 and 225 mm in length.

The retrieved fish were moribund by the time they reached the decks (hearts fibrillating and weak reflexes), but showed little trauma compared to others, such as *Benthosema*. Air emboli in the circulatory systems was a probable cause of morbidity. Whole fish were fixed immediately after retrieval by total immersion in cold 3% glutaraldehyde buffered to 7.4 pH with 0.1 *M* sodium cacodylate at refrigerator temperature (*ca.* 4.0°C). Specimens were stored in a refrigerator, and the fixative was replaced with fresh fixative after about 12 h. After 2–3 days, the fish were finally stored in 1% glutaraldehyde in 0.1 *M* cacodylate. Dissection of photophores, post osmication, and embedment in epoxy resin of tissues for future study were made shortly after returning to port.

Thick (1 micron) epoxy sections for light microscopy were stained with methylene blue-azure II. The light micrographs in Figures 3, 11, 15, and 17 were made with a Zeiss Axiophot microscope. Thin sections for electron microscopy were stained with uranyl acetate, followed by Reynolds lead citrate, and were studied with a Zeiss 10 electron microscope.

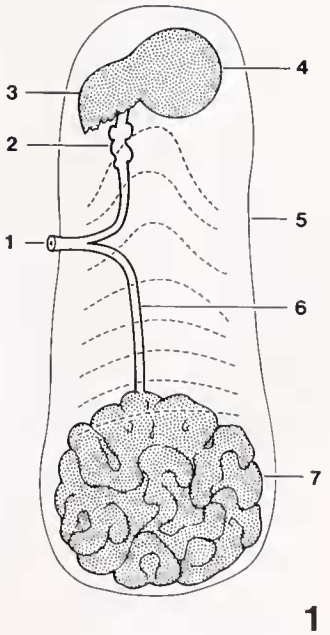


Figure 1. Diagram of an entire photophore complex [from the upper serial row (OA)] as viewed through the surface of the fish. (1) Joint secretory duct orifice to external surface. (2) Secretory duct of gland D with attached clusters of secretory cells. (3) Lateral hemispheric canopy of gland D. (4) Gland D. (5) Transparent collagen covering shield. (6) Secretory duct of gland V. (7) Gland V. Dashed lines indicate the pattern of overlapping rows of dioptric material (see Fig. 17) that lie immediately under the shield.

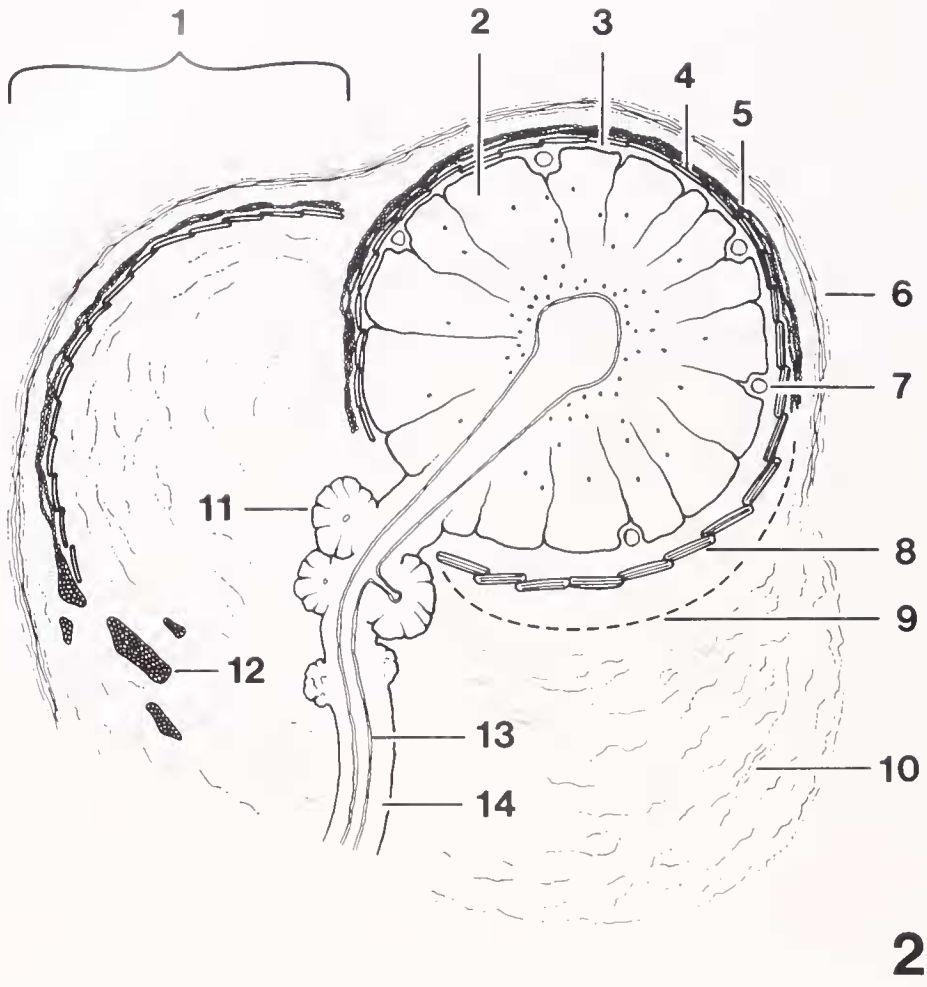
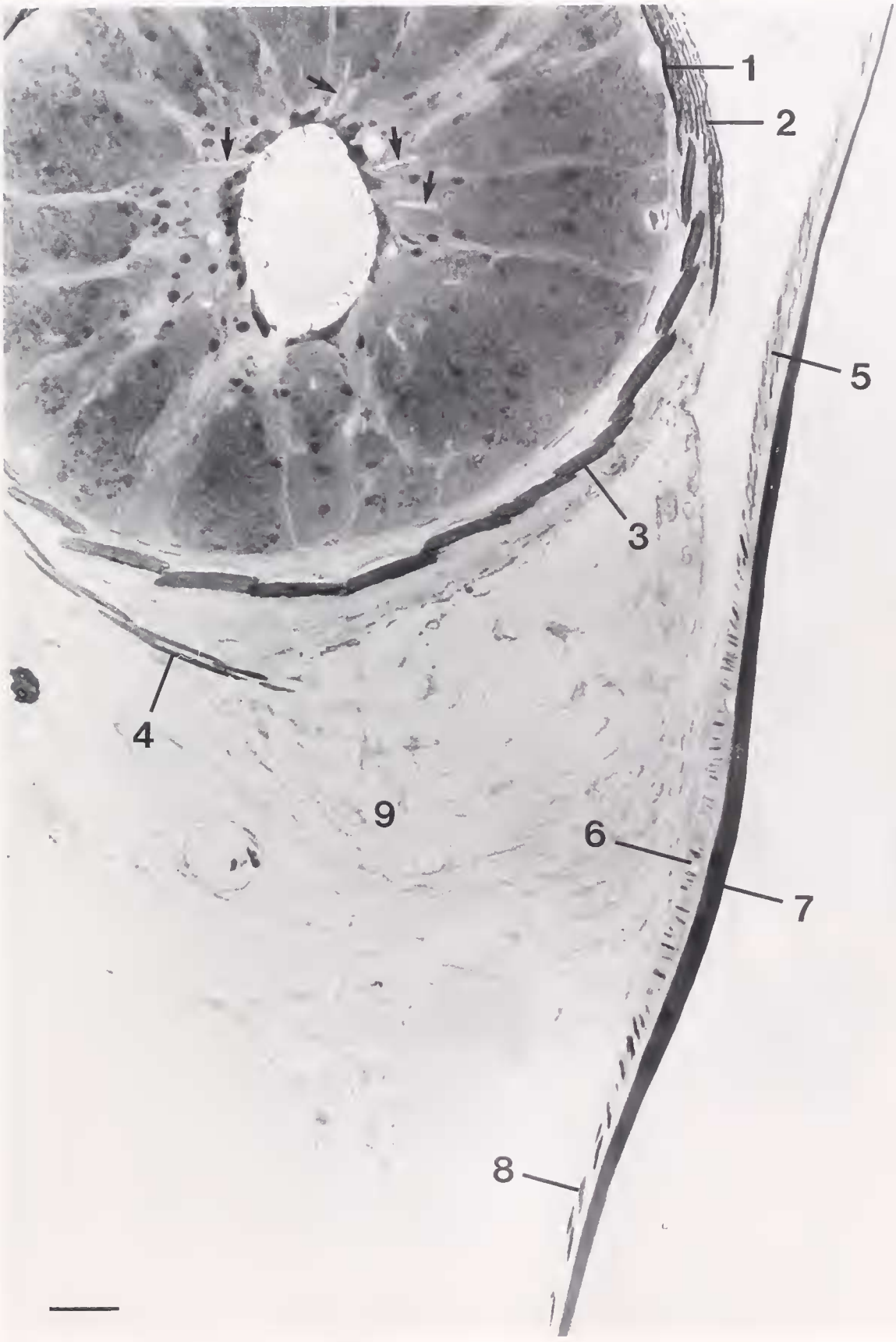


Figure 2. Diagram of gland D, same orientation as in Figure 1. (1) Canopy with outer connective tissue layer, a middle layer of iridosomes and an inner layer of thin platelets composed of laminations of dioptric material. (2) Radiating spindle shaped cluster of secretory cells arranged in packets of five or six cells. (3) Thin layer of connective tissue. (4) Layer of thin dioptric platelets similar to the layer in the canopy. (5) Beaded layers of oriented iridosomes (see Fig. 7a). (6) Layer of connective tissue that encompasses both gland D and its canopy. (7) Blood vessel. (8) Thick laminated dioptric facet (see Figs. 3, 10, 11). (9) Location of a continuation of the platelet layer that drops down in back of gland D forming a cup-like shelf that terminates near the plane of section, *i.e.*, the free edge faces the surface of the fish (see 4 in Fig. 3). (10) Oriented layers of sparse, flattened connective tissue cells (see Fig. 8) embedded in finely granular lucent material that extends from under the canopy to form a lenticular bulge. (11) Cluster of secretory cells similar to those within the gland proper but on a smaller scale. (12) Small clusters of cells containing irregularly arranged iridosomes. (13) Epithelial layer of secretory duct. (14) Connective tissue sheath of secretory duct.

Figure 3. Light micrograph of gland D. Plane of section is at right angle to the diagram in Figure 1, *i.e.*, at right angle to the surface of the fish. (1) Thin laminated dioptric platelets. (2) Sheets of beaded melanin-like iridosomes. (3) Thick dioptric plates or facets. (4) Shelf of thin dioptric platelets continuing from the posterior-ventral edge of layer 1; its out of plane position is indicated in Figure 2 by dashed line. (5) Overlapping dioptric material, closely packed. (6) Dioptric material, more dense, and oriented at right angle to the lens of the shield. (7) Lens-like thickening of the shield. (8) Cross section of overlapping dioptric ribbons that range on down to the level of gland V (see dashed lines in Fig. 1). (9) The main bulge of lenticular material. The curving layers of connective tissue help to maintain the symmetry of the bulge. Collecting channels of the secretory cell packets are indicated by arrows (also see Figs. 5, 6). Scale bar = 20 μm.



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Light microscope studies of whole mounts were made by two methods. First, reasonable detail could be seen when the flat, embedded epoxy blocks were placed on a slide and observed through the upper (shiny) surface with the 10× and 40× objectives of a compound microscope. The osmium tetroxide in the post osmication process acted as a stain. However, the best whole mount preparations were obtained after the melanin pigment had been bleached away (1% chromic acid in 1% calcium chloride, 6 to 12 h at room temperature). The tissues were then stained in Lynch's precipitated borax carmine, followed by dehydration and mounting on slides with Permount.

An additional effort was made to reveal the internal fine structure of the iridosomes, which, although "melanin-like," resisted bleaching with chromic acid. Treatment with the more potent peracetic acid (Barka and Anderson, 1963) to the point of tissue maceration produced no marked bleaching. Some visualization of internal ultrastructure was obtained only by use of very thin (grey) sections. Several attempts were made to demonstrate nerves with Protargol (Winthrop Chemical Co.), but the efforts were not successful. Because silver stains for nerves are notoriously capricious, the failure does not indicate that nerves are absent.

Results

The serial photophores of *Gonostoma elongatum* are arranged in two rows on the ventro-lateral side of the body. The upper serial row (OA) runs from the operculum to the anal level, and each photophore includes two glandular structures. The lower row (IV, VAV, AC) runs the full length of the body and each has only one structure. (For diagrams and keys to the photophores of *Gonostoma* see pp. 284 and 300 in Badcock, 1984.) Each of the upper serial photophores has two distinct glands (Fig. 1). Each gland has a duct that joins the other, and the common duct exits by an orifice to the surface of the fish. The whole glandular complex is covered by a transparent shield of multilayered collagen. The common secretory duct empties to the external surface close to the posterior edge of the shield. For convenience, the dorsal gland is referred to as "gland D," and the ventral gland is called "gland V."

A faint, bluish light was observed along the ventrolateral aspects of several *G. elongatum* in a darkened room aboard ship, but I did not have equipment to localize or enhance the light source. Also, admittedly, my primary concern was to initiate fixation as quickly as possible.

Gland D

Gland D is spherical and composed of long secretory cells radiating from a central collecting cavity (Fig. 2). The cavity is lined with epithelial cells that continue on to form the lining of the secretory duct. The radiating cells are grouped in clusters of 5 or 6 in such a way that the central adjoining membranes of the cluster form a channel (Figs. 5, 6) that connects to the central collecting cavity. (The term "channel" is preferred over "duct" because there is no epithelial lining present.) The lateral surfaces of each spindle-like cluster of cells borders on areas filled with connective tissue and blood vessels (Fig. 4).

Each glandular cell is filled tightly, in an oriented fashion, with secretory granules and multiple layers of rough endoplasmic reticulum (RER). The RER is layered parallel to that part of the cell adjacent to the connective tissue space (Fig. 4) and fills the outer, more broad end of the cell. The secretory granules are found in that part of the cells adjacent to the common channels (Fig. 5), and that association persists to the point where the chan-

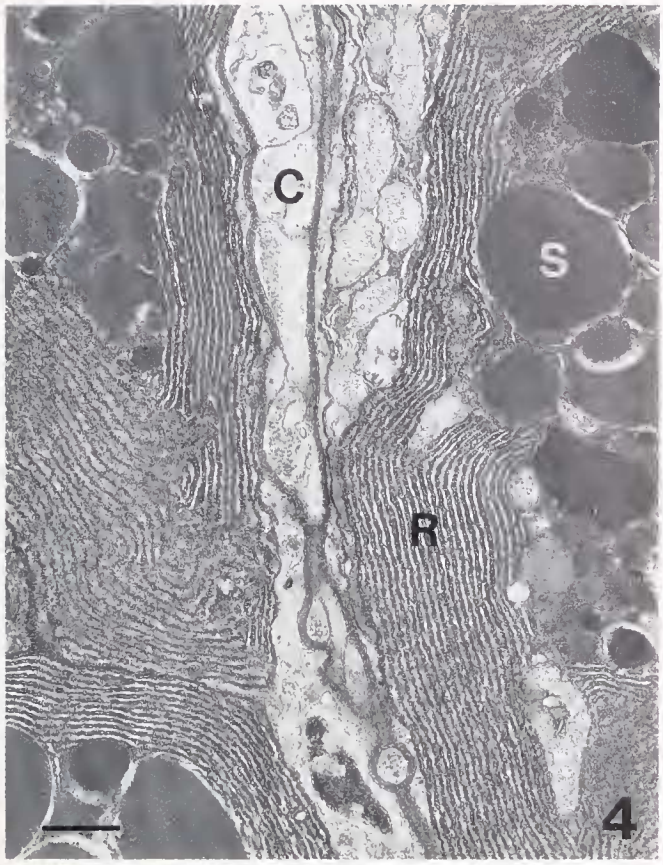
Figure 4. Longitudinal section along a radius of gland D, including the surfaces of two cells from adjoining packets of cells, and together with intervening connective tissue and vascular supply (C). Rough endoplasmic reticulum (R) lies parallel to the cell surfaces facing the connective tissue. Large secretory granules (S) are located away from the connective tissue layers and are found adjacent to the secretory channels in the middle of the packets (see Fig. 5). Scale bar = 1 μm

Figure 5. Cross section near the midpoint of a radiating packet of secretory cells in gland D. Secretory granules (S) are packed about a central collecting channel (C). There is no tubular epithelium but the glandular cells do have tight junctions (twin arrows) and desmosomes (single arrow). Scale bar = 1 μm

Figure 6. Section closely parallel to the central collecting cavity of gland D cutting through the epithelium lining which has dense nuclei (Nu) and dense cytoplasm. Each packet of radiating glandular cells (G) narrows and penetrates the epithelium so that the collecting channels (C) connect to the central cavity. At this level, secretory granules are predominant in the secretory cells. Scale bar = 1 μm

Figure 7a. Flattened, oval-shaped iridosomes held in orderly fashion by parallel membranes having cross bridges. They are quite dense, and both chromic acid and peracetic acid treatment failed to bleach the melanin-appearing granules. Scale bar = 0.27 μm.

Figure 7b. Higher magnification of Figure 7a (which is an extremely thin section) with enhanced contrast to reveal the faint laminations that are registered parallel to the bounding membranes of the iridosomes.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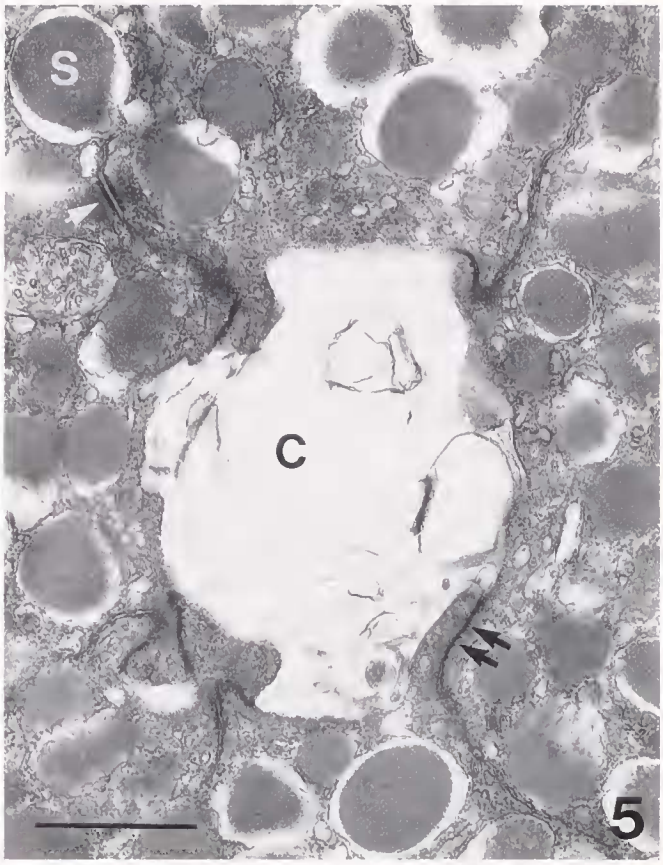
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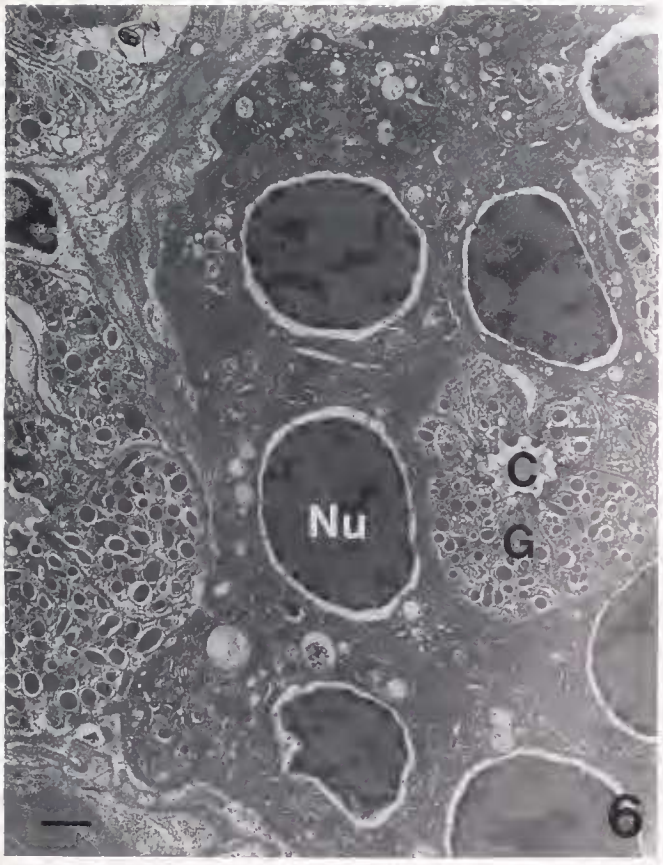
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nels empty into the central secretory collecting cavity after penetrating the epithelial lining (Fig. 6).

The secretory duct immediately adjacent to gland D has small clusters of cells attached to it. The cells are secretory and similar to those in the main part of the gland in having plentiful RER and secretory granules. They differ only in being more rounded and having very short collecting channels (Fig. 2). The base of the secretory duct and its attached cluster cells is covered by a cup-like hemispheric "canopy" extending laterally from the spherical gland (Fig. 2). The dorsal three quarters of gland D is covered by a double layer, the innermost being composed of a thin layer of laminated, dioptric platelets (Figs. 2, 3); [structures in this article that respond to polarized light are called "dioptric" (see Fig. 12)]. The outer layer is composed of beaded rows of melanin-like iridosomes (Figs. 2, 3, 7). A similar double layer also extends over the inner surface of the canopy. Irregular cellular clusters of iridosomes are found at the free edge of the canopy (Fig. 2).

The dioptric platelet layer covering gland D extends down on all sides, slightly more so on the ventro-medial side where it forms a narrow shelf or band (out of plane of section in Fig. 2, but seen in Fig. 3). The lower surface of the gland D lacks iridosomes and has a circular pattern of dioptric material forming thickened, multilayered plates or facets. The facets slightly overlap each other inward to the central dorso-ventral axis of the gland (Figs. 2, 3). The facets, when viewed with transmitted light in epoxy embedded material, can be seen to form a brilliant blue pattern resembling that of mosaic tile. The facets are composed of orderly, multiple layers of membrane-bound material (Figs. 10, 11), which presumably accounts for the response to polarized light. All of the other dioptric materials mentioned in this article have similar layering.

The iridosomes are small, flattened, lozenge-shaped particles with their long axes held in register by membranes. The result is a sheet of iridosomes that in cross section looks like a beaded necklace (Fig. 7). The outer layer covering gland D is composed of many sheets of such material. The pigment of the bead-like iridosomes is quite resistant to chromatic acid digestion and responds only slightly to the more corrosive peracetic acid. It probably is not representative of the usual melanin. A multiple layering of material can be seen within the matrix of the ovoid iridosome particle. The layers are parallel to the free surface of the beaded sheets of iridosomes and can be visualized only in very thin (grey in color) ultratome sections.

The space covered by the canopy is filled with an orderly arrangement of loose connective tissue (Fig. 2). Sparse, oriented, flattened cells (Figs. 8, 9), supported by some random collagen, fill the cavity and extend ventrally. The ventral extension expands into a bulge underneath gland D (Figs. 2, 3). Because of its spherical shape, and because a better designation is lacking, I call it a "lenticula." It has a fine glandular matrix that is completely transparent in preserved material. Where the lenticula adjoins the covering shield the concentration of collagen in the matrix markedly increases (Fig. 9).

The secretory cavity of gland D is emptied by a duct that also connects to a similar duct from gland V (Fig. 1). The common duct then exits through the epithelial surface of the fish (Fig. 12). The cavity and the ducts are lined with a distinct epithelium characterized by dense nuclei (Fig. 6). A layer of connective tissue surrounds both ducts, and the lumen of each duct contains a glandular nondescript material.

Gland V

The plate-shaped gland V is anatomically and cytologically different from gland D. The secretory cells form a single layer adherent to a network of thin-walled interconnecting capillaries. The labyrinthic space between the capillaries (with their adherent cells) is packed with secretory material (Fig. 13). There is no collecting chamber, and the duct for gland V is attached directly to one of the upper (dorsal) arms of the sprawling labyrinth that contains secreted material. The cells of gland V have obvious

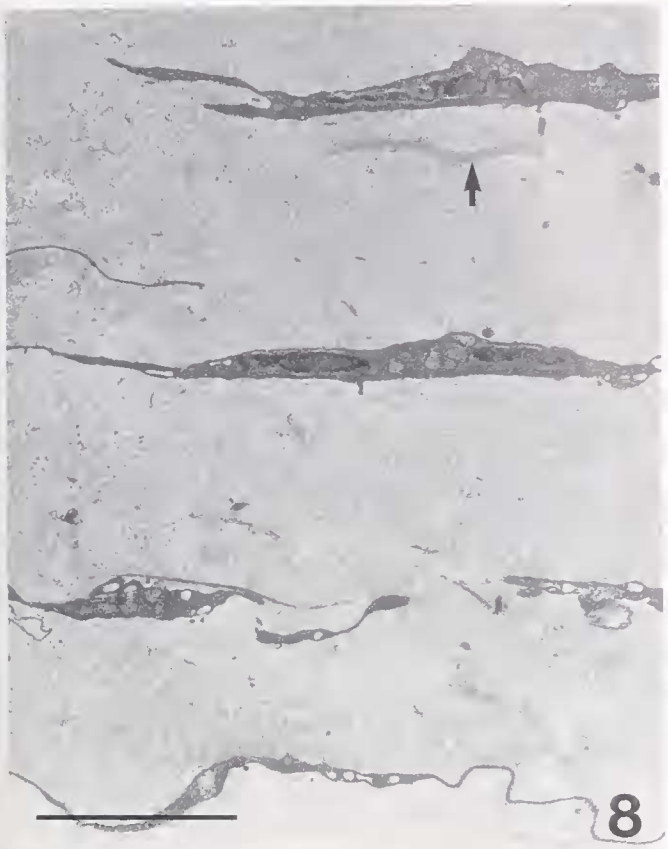
Figure 8. Cross section of flattened connective tissue cells in the transparent bulge (lenticula) located below gland D. Note oriented parallel array. Small clusters of collagen fibers (arrow) are barely visible at this magnification. Matrix is of fine amorphous material. Scale bar = 20 μm.

Figure 9. Higher magnification of the lenticula as it adjoins the covering shield. Collagen fibers (asterisk) are much more numerous and the connective tissue cells are larger and more irregular. Arrow points in the direction of the attachment to the covering shield. Scale bar = 5.0 μm.

Figure 10. Cross section of a multilayered dioptric facet of gland D. Note the regular periodicity of the layer being sequestered from a parent cell (arrow). Scale bar = 1 μm.

Figure 11. Multilayered dioptric facets of gland D illuminated by polarized light. Strong response is obtained. Also, note the overlapping arrangement of the plates (see Figs. 2, 3). Scale bar = 1 μm.

Figure 12. Longitudinal section of the lips of the common secretory duct as it exits to the externum of the fish. Scale bar = 10 μm.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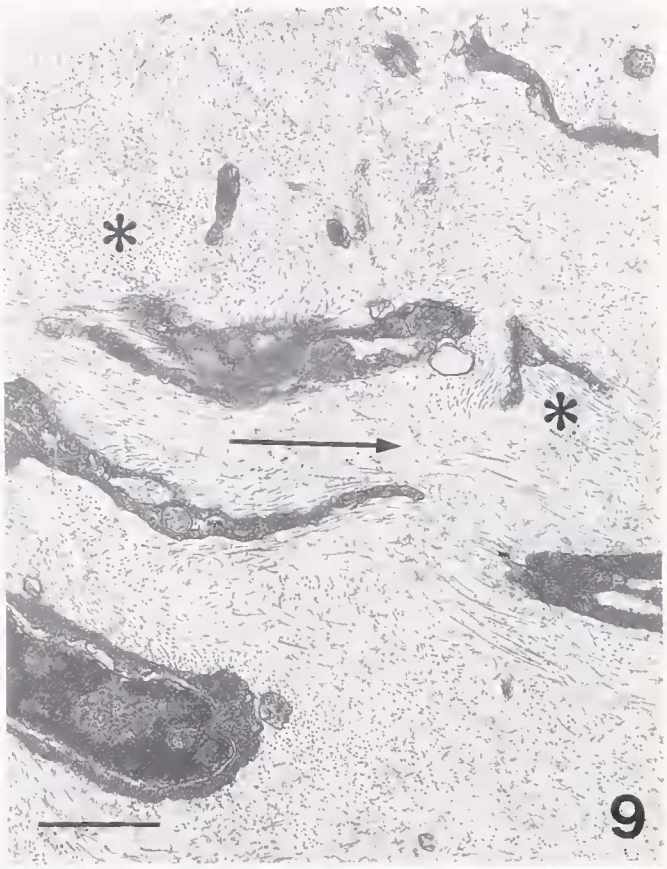
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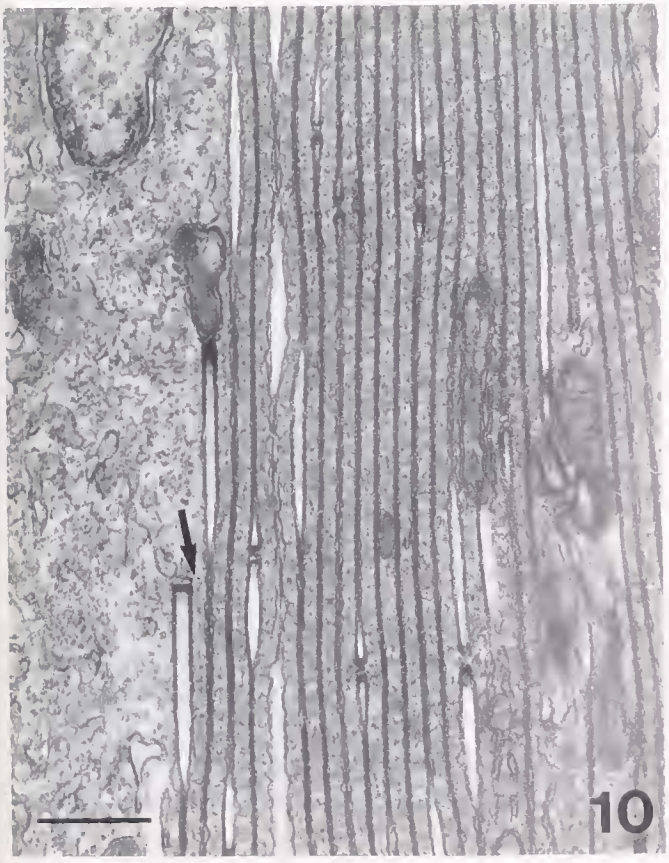
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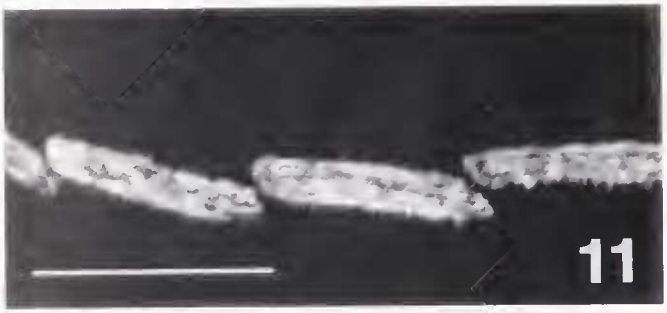
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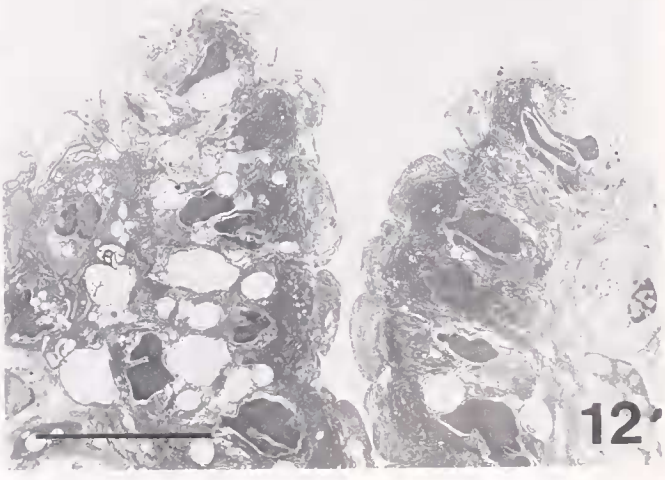
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secretory elements such as granules and rough endoplasmic reticulum (Fig. 14). The number of secretory granules and the number of cells having the granules is quite variable. Cells possessing granules are usually distributed in a gradient, the cells having the highest concentration of granules being found at the upper (dorsal) end of the gland.

Gland V has dioptric material in a layer immediately under that organ (Fig. 15). It is in the form of thin rectangular ribbons overlapping and randomly disposed with no prevailing orientation when viewed in embedded material by light microscopy. Each ribbon is about 20 × 100 μm and has four or five layers of laminated material similar to that in Figure 10. The ribbons probably provide the whiteish, silvery reflection seen in the living, though moribund, animal. Sometimes the reflection has a faint yellow color in fixed material.

Shield

The entire dual gland complex is covered by a transparent shield (Fig. 1) of collagen orientated in alternating layers that are at right angles to each other (Fig. 16). Fifteen or so of the layers form a lens-like thickening at the level of gland D (Fig. 3). The number of layers drops off in all directions until there is only one layer of amorphous material at the edge of the shield. That periphery is embedded in a rod-like rim of cellular material (Fig. 18). The free surface of the shield is covered by a thin layer of epidermal epithelium that is frequently lost during collection and preparation.

Immediately beneath the shield is oriented dioptric material arranged in rows parallel to each other (dotted lines in Fig. 1). The rows of ribbons overlap in a steeply pitched, shingle-like fashion (Fig. 17). The angle of the pitch is downward, *i.e.*, laterally and ventrally to the body. The region of layered shingles reaches from about the median level of gland D (Fig. 3), down to the upper edge of gland V (*i.e.*, it does not cover gland V). The parallel rows of dioptric material extend straight across the shield just above gland V level, but as the gland D level is approached, the rows increasingly bulge upward (Fig. 1). There is a regional change in the orientation of the shingles where the connective tissue of the lenticula adheres to the shield. In that region, the dioptric material is more coarse and oriented at right angles to the shield (Fig. 3). The modified shingles lie between the lens of the shield and the lenticula of gland D. Above that region, the dioptric material again slants downward, is more compact, and ends. Although the light microscope cross sections of the shingles responded to polarized light, at no time was color or reflection evident in the intact animal, living or fixed. The dioptric material is transparent and can easily be overlooked at the light level unless differential interference contrast (DIC) lighting of embedded material is used.

Comparison with some other types of photophore in G. elongatum

The lower serial row, the suborbital, and the caudal photophores each have a gland that, in size and cytology, is similar to gland D. However, the lower serial photophores have no gland V; the singular gland D connects directly to the surface via a single duct. Both the suborbital and caudal photophores have gland V type tissue, but noteworthy in each case, the glands V and D are connected directly to each other by a duct that does *not* approach the surface.

Discussion

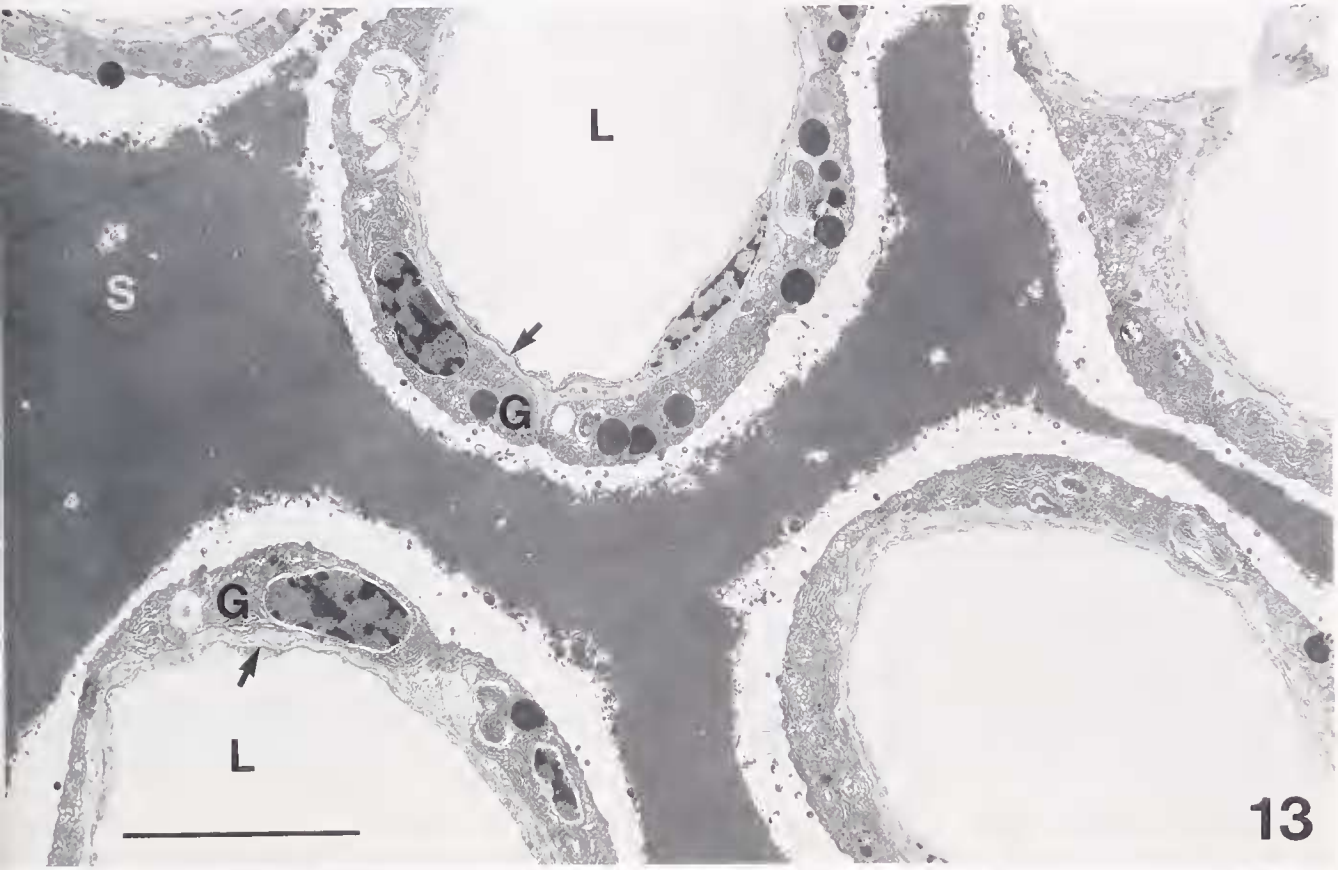
Gland D and its dioptric material

Herring and Morin (1978, p. 306) have provided (after Bassott) a line drawing of gland D in *Gonostoma* at the light histology level. They diagram the radiating arrangement of secretory cells focussed on a central collecting cavity and say that a duct connects to the surface of the fish, but do not show a clearly organized duct or associated cluster cells. Also, items such as canopy, facets, and lenticula are not depicted, and gland V is not mentioned. Gland D of *Gonostoma* is better illustrated in a micrograph by Nicol (1969, p. 365). The

Figure 13. Cross section of several thin-walled capillaries (arrows) in gland V. The capillaries form a flattened irregularly branching, network of vessels and are covered by a single layer of glandular cells (G). The labyrinthic space between the capillaries is filled with secretory material (S). The capillaries are distended, and the lumen (L) is empty of red blood corpuscles because of emboli located somewhere else in the system. Scale bar = 10 μm.

Figure 14. Detail of a secretory cell in gland V. Note usual glandular characteristics such as rough endoplasmic reticulum (R), Golgi apparatus (G), and secretory granules (S) and secreted material (asterisk). Also, note the irregular protrusions of the cell surface that may aid in secretory release. Scale bar = 1 μm.

Figure 15. Light micrograph of a section through the layer of dioptric ribbons that lay beneath gland V. The ribbons are thin (4 or 5 laminations), rectangular (about 20 × 100 μm), and randomly disposed within the layer. Cross section of a ribbon (single arrow) and longitudinal section (twin arrows). Scale bar = 20 μm.



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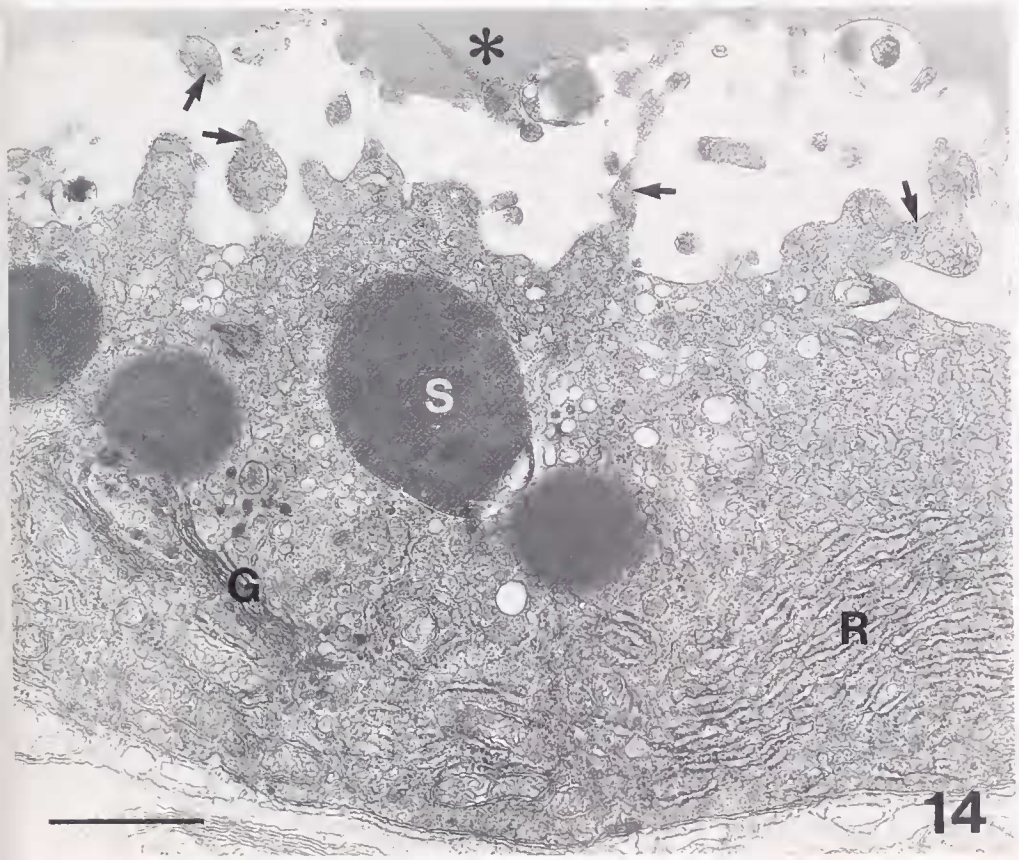

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photophore is from the "lower trunk." If trunk is defined as post-anal, then the photophore is one of the lower serial row that has no gland V (the upper serial row of dual gland photophores is on the abdomen anterior to the anus). However, because gland D in the upper and lower serial rows are quite similar, the photograph by Nicol is comparable to the gland D described here (but not in as much detail). The secretory cells of gland D are equivalent in all respects to the A photocytes of Bassott (1966). However, I found no cells equivalent to his type B photocytes. The lack of type B cells in the photophores of gonostomids has been noted by Bassott (1966) and Nicol (1969).

Gland D is capped with a layer of dioptric platelets backed by a layer of iridosomes in such a manner that light can be reflected ventrally and laterally toward the external surface, a common phenomenon in photophores located laterally on the body. These layers may selectively reflect spectral light (Denton *et al.*, 1985). The canopy, as an auxiliary structure, may have a light concentrating role. The layer of dioptric platelets, plus iridosomes, could have a reflective and light concentrating effect. It is in a position suited to reflect some light from gland D and much of the light from the cluster cells at the base of the collecting duct. The slightly overlapping, concentric arrangement of the dioptric facets on the ventral side of the sphere could have a concentrating effect as well as a possible light filter effect similar to that described by Denton *et al.* (1985). Furthermore, the shelf of dioptric platelets (Figs. 2, 3) that slopes toward the shield could provide a deflecting effect, guiding more light through the lenticula into the lens.

Lenticula as a light collector and anchor

The lenticular tissue is in the shape of an inverted comma with the tail under the canopy and the spherical bulge positioned below the gland proper (Fig. 2). The highly oriented loose connective tissue and amorphous matrix could allow for an optically clear structure with an index of refraction suitable for concentrating light. The tissue might also act as a light filter (Denton *et al.*, 1985). Bassott (1960) describes a photophore in the closely related gonostomatid *Maurolicus* that has a body that is gelatinous, transparent, homogeneous, and refractive; and suggests that it may act as a lens. The oriented collagenous attachment of the lenticular apparatus to the shield could serve two purposes. The most obvious would be to pass light to the lens of the shield in a registered fashion. The other purpose, in lack of other connective tissue, would be to serve as an anchor for gland D, keeping it oriented and in place.

Gland V and its dioptric material

Although gland D in *Gonostoma* has been repeatedly identified in the literature as a photophore and considered as furnishing a taxonomic pattern (Grey, 1964), the associated gland V has received little attention. One of the first to identify it was Brauer (1908), who referred to it as a "sack formigen Organ." It has been referred to as being glandular and having a direct connection to gland D, but there is no description of the two secretory ducts fusing into a *common* duct to empty to the surface. Also, I find no cytological descriptions of the gland V.

The secretory cells of gland V have little or nothing in common with the secretory cells in gland D, either anatomically or cytologically. The type cell of gland V has a well-developed Golgi apparatus and associated granules that indicate the usual merocrine type of secretion. However, granules do not approach the dense population seen in gland D.

There is no evidence in the literature suggesting that gland V produces luminescence. Most certainly it has no category "A" photocytes as found by Bassott (1966) in a broad spectrum of photophore types in teleosts. The dioptric ribbon-like material beneath gland V must serve as a reflector, and account for the silvery appearance.

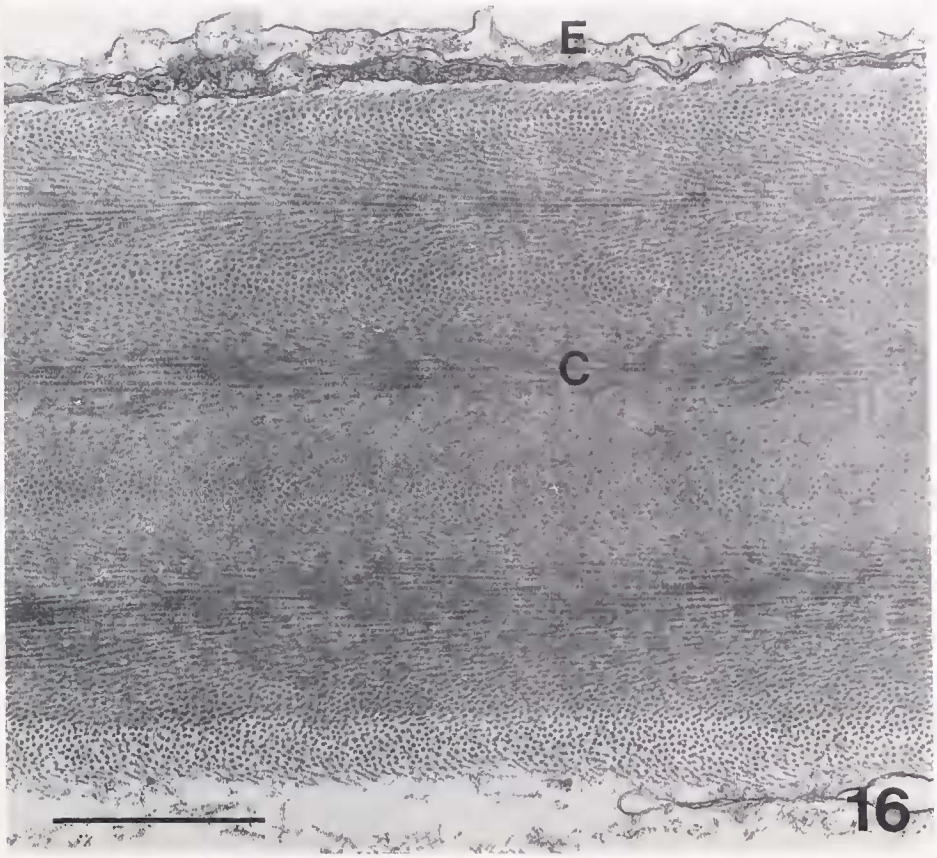
The shield and its dioptric material

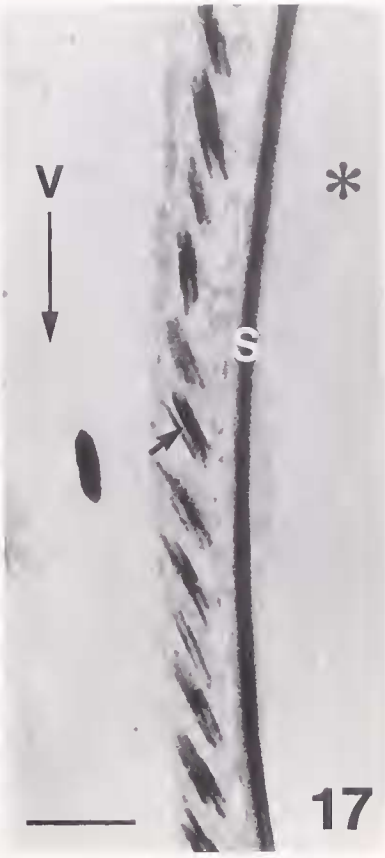
The shield is composed of multiple layers of collagen, each arranged at right angles to the neighboring layers. Thus, maximum stiffening is obtained. The shield is further strengthened at the tapering circumferences by a rod-like rim of cells. The thin overlying cutaneous epithelium is easily displaced in dissection and probably does not contribute much strength to the system.

The shield may be involved in two aspects of light release. First, the shield itself is thickened to form a lens, albeit it may be weak. That lens is positioned directly opposite and attached to the lenticula of gland D, so that light passing from the lenticula may be collected by it. Second, the oriented rows of dioptric material associated with the shield may have indices of refraction that would help to guide light downward from gland D (with a possible exception at the level of the lenticula). The rather complicated orientation of the rows in relation to gland D, straight rows transitioning to curved, supports this interpretation. Moreover, there is no such dioptric material accompanying the shield over gland V. Whatever the function of the dioptric material associated with the shield, it must be in reference to gland D.

Iridosomes

Bassott (1966) describes the photophores found throughout the stomiatoidei (which includes *Gonostoma*)





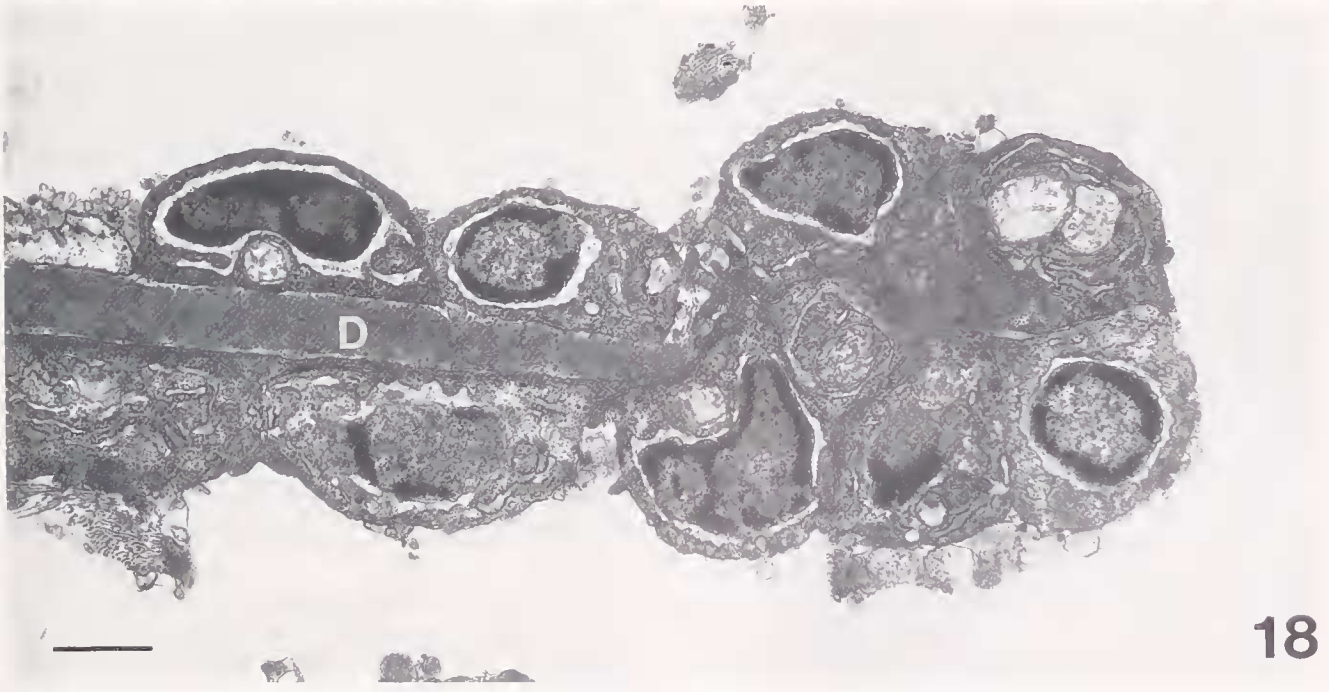


Figure 16. Cross section of the shield, median between its free edge and the lens thickening. Note that the alternating layers of parallel collagen fibers are at 90° angles to each other, thus adding strength to the shield. Collagen (C). Skin epithelium (E). Scale bar = 1 μm.

Figure 17. Light micrograph of a cross section of the dioptric ribbons that lay in overlapping fashion immediately under the shield. (See Fig. 1 for their distribution). Ventral direction (V). Collagen shield (S). Dioptric material (arrow). External medium (asterisk). Scale bar = 10 μm.

Figure 18. Cross section of the edge of the collagen shield. The shield proper tapers peripherally to a narrow flange of dense material (D), almost devoid of collagen fibers, and is finally bordered by a rod of supporting cells that may have participated in the growth of the shield. Scale bar = 1 μm.

as "urn, sphere or retort shaped." The wall of the sphere is always formed of reflector cells which, in turn, are coated with a "layer of iridocytes of melanine" (Bassott, 1966, p. 566). The particles in Figure 7 could be called "melanosomes" because they look melanin-like and have no proven iridescence. However, the particles, by reason of their laminated substructure, their rigid orientation within sheets, and their resistance to chromic acid and peracetic acid digestion, may not be usual melanin granules. For example, Nicol (1989) describes two kinds of "melanoid substances" to be found as chemical components in the reflectors of fishes. He uses the term "melanoid" because the two are chemically derived in part from tyrosine by tryosinase catalysis and exhibit certain parallels to melanin synthesis. By precedent, the term "iridosome" is chosen in this article as representing the particles within the "iridocyte" of Bassott.

The sheets of iridosomes are ideally located about gland D and under the ribbons of gland V for a possible light modifying function. The hitherto unreported laminations in the particle, plus their orientation to the long axis of the sheets, suggests that such could be true. (On the other hand, they may be exceptionally efficient light suppressors.)

Functional aspects

I approach the discussion of possible functions with trepidation, and I quote Buck (1978, p. 420): "At least 20 functions of bioluminescence in one animal or another have been proposed—Though often quite plausible, most of these proposals were originally more a reflection of the ingenuity of observers than of the solidity of the observations, and there has been an unfortunate tendency for later authors who are casting about for functions of luminescence in their own material simply to list possibilities without adducing any additional support." This comment is particularly appropriate when considering the mesopelagic fish, which are difficult to observe or to test in any way.

Doubtless, type D gland photophore luminesces. Swift *et al.* (1977) recorded luminescence in a *Gonostoma* photophore, "about 2/3 of the distance from the head to the tail." That distance would locate it in the area of the body that has only lower serial photophores with gland D (see illustration, Badcock, 1984, p. 300). Furthermore, Anctil (1972) has stimulated luminescence in the photophores of the closely related gonostomid, *Maurolicus*.

I find no record where gland V is given the status of a photophore. However, the enlarged type V gland tissue in the caudal gland of *G. elongatum* has been referred to as "luminous tissue" by Grey (1964), and it has associated with it, at a tangent and relatively inconspicuous, type D gland that is cytologically akin to the lower serial photophore that has been proven to luminesce (as stated above). Thus, both glands D and V may produce light. Keeping Buck's admonition in mind, one would add that proof for a luminescent function for gland V is faint.

The possibility that luminescence may occur other than in gland D or gland V (*i.e.*, in surface slime) cannot be discounted. Bassott (1966) says of *Gonostoma* that the absence of clearly characterized B cells in association with the A cells could be explained by the possibility that the A cell secretion is secreted to the outside and there mixed with other agents. Also, Swift *et al.* (1977, p. 822) quote Brauer (1908) and say "the light organs in *G. elongatum* have ducts leading externally which suggests along with the large value of FWHM (Table 1) that its spectra show little effect from the masking of overlying tissue." The implication is that the ducts bring the luminescence to the surface, where it is more easily seen. My own observations of the faint bluish luminescence in *G. elongatum* were not sufficient for a specific localization of source. I hazard no thoughts regarding the function of a direct ductal connection between glands D and V in the suborbital and caudal photophores. It is interesting that, at least in *G. elongatum*, gland V is always associated with a gland D. However, gland D is not necessarily associated with gland V.

One of the noteworthy features of this article is the detailed analysis of a whole array of dioptric materials that can efficiently handle the luminescent light in such a way as to produce a downward, evenly diffused lighting for the fish, that could function as counterillumination.

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